

FURTHER NOTES ON CANNIBALISM AMONG  
LARVÆ

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In a previous communication (Dethier, 1937) most of the reported cases of cannibalism among lepidopterous larvæ were discussed. Hunger and crowding, with thirst as a contributing cause were found to be the prime factors inducing this anomalous diet. This confirms the conclusions of Hering (1926) whose book was previously unavailable to the writer. The present notes offer further explanatory data pertaining to hunger and crowding as causes of a meat diet. The effects of such a diet and the ability of a phytophagous larva to survive on one are considered. Additional cases are also cited.

## I

In an effort to understand more fully the various causes initiating cannibalism and the carnivorous habit in general among lepidopterous larvæ the following experiments were designed.

Two final instar larvæ of *Estigmene acrea* Drury and one last instar larva of *Isia isabella* A. & S. were placed in a dry jar approximately twenty inches in volume. Also placed in the jar were one pupating *E. acrea* larva from which the cocoon had been removed, a smaller arctiid in similar condition, and one freshly killed *I. isabella* larva which had been slit open longitudinally. The experimental animals had neither eaten nor drunk for four days. It was observed that they crawled ceaselessly around the bottom of the container exploring the surface with their antennæ and mouthparts. Some dry fæces when encountered were nibbled at slightly. No unusual behavior occurred until the slit carcass was encountered. Here the live animals immediately sucked up the body fluids. After a period of five minutes all three

experimentals were eating the tissues of the exposed larva. Next a decapitated *Encoptolophus sordidus* Burm. was placed in the jar. Its metathoracic legs were removed to prevent kicking. The grasshopper was investigated by the larvæ but no attack made upon it; however, when the carcass was slit open, the larvæ that chanced upon it started feeding almost immediately. The flesh, the eggs contained within the abdomen, and as much of the cuticle as was not too heavily sclerotized were eaten. At this stage the small pupating arctiid was also eaten by the *I. isabella*.

It can be seen from these observations that larvæ are more readily attacked and eaten when their tissues are exposed. It is to be expected that caterpillars would be more attracted to exposed tissues because there is a more concentrated odor arising from them than from an insect completely sheathed in cuticle. Also, there is no stimulation of the mouthparts by an unmutilated carcass. On the other hand, body juices exposed to the air may stimulate the mouthparts directly. Further there is the possibility that larvæ partaking of body juices are prompted to do so by thirst. An unmutilated carcass is attacked only when the larvæ reach such a degree of starvation that they bite frequently at near-by objects.

In order to ascertain the exact series of events occurring when an animal with cannibalistic or carnivorous tendencies approaches another larva, a single live naked noctuid larva was placed in the jar with one *E. acrea*. In the limited area the two frequently encountered each other. The *E. acrea* had reached the stage in which it bit at all objects encountered. When it endeavored to take several bites of the noctuid, however, the latter thrashed about vigorously. Although the arctiid stabbed viciously at its intended victim several times, it finally withdrew. The noctuid's cuticle had not been pierced. On numerous occasions the same process was repeated. Finally the noctuid was rendered more or less quiescent by the buffeting of the more active and aggressive arctiid. In this quiescent state, more or less bathed in its own regurgitated juices and those of its attacker, the noctuid was eaten. Undoubtedly this procedure takes place in most instances when one live insect is eaten by another. The higher percentage of cannibalism noted under crowded

conditions (Dethier, 1937) may be explained by the fact that chance meetings are more frequent. When similar conditions were reproduced in a cage twelve by sixteen inches, both animals eventually died of starvation.

While experiments with mutilated animals indicate that thirst may be one factor in inducing cannibalism, the following experiments demonstrate that hunger by itself is an important factor.

One *E. acrea* was kept in a moist atmosphere, given its fill of water, and presented with every opportunity to continue drinking. When given a mutilated larva of the same species the experimental animal began feeding almost immediately. Repetitions of this experiment prove that hunger as distinct from thirst is one factor in inducing a carnivorous diet.

The experimental animals never chose a diet of meat in preference to plants. Plant food was always accepted even after the larvæ had gorged themselves with meat. In three hours a single *E. acrea* consumed one *E. sordidus*, another consumed one entire *Gryllus assimilis* Fab., and an *I. isabella* consumed one full-grown larva of *Vanessa virginiensis* Drury. These three arctiids pupated and produced normal adults.

With regard, therefore, to the rôle played by hunger and crowding in causing cannibalism the following conclusions seem justified: First, the degree of hunger is of considerable importance. Larvæ in the initial stages of hunger are not readily induced to eat flesh unless stimulated probably by the odor of the body fluids and more certainly by direct contact with them. Larvæ in the final stages of starvation yet still active enough to crawl about do not require such an intense stimulation. Since animals in this condition habitually nibble at near-by objects, they eventually bite through the integument of an intact carcass or a quiescent animal. At this juncture they too are stimulated by the flesh within. An exceedingly active victim is not actually eaten till it has been rendered more or less quiescent although it may still be capable of considerable movement. Second, crowding facilitates the initiation of the events already mentioned as caused by hunger. In addition crowding induces attacks not prompted by hunger (Balduf, 1931; Dethier, 1937).

## II

It was observed that relatively large blocks of tissue were present in the fæces of these carnivorous larvæ. In order to facilitate the examination of these tissues to determine what benefit the larvæ were deriving from their diet the fæces were preserved in alcohol, sectioned in paraffin, and stained with Delafield's hematoxylin and eosin.

Examination revealed that the tracheae as well as all other chitinous structures had passed through the alimentary canal completely untouched. This was to be expected since the occurrence of an enzyme acting upon chitin is very limited (Uvarov, 1928). Epithelium had been completely broken down. Relatively large blocks of muscle tissue were present in the fæces. These were recognizable as such; but digestion had been more or less complete, nothing remaining but a faint indication of the muscle fibers. No conclusion could be drawn concerning the fate of fat due to the histological procedure employed. Plant material from the gut of the victim was also present in the fæces. Serial sections revealed that cell walls in the majority of cases were intact although the entire contents had been removed. This is in accord with Biedermann's (1919) contention that all the active components of the digestive juice can diffuse through cell membranes.

In order to throw further light upon the situation, larvæ were tested for the presence of various digestive enzymes. Tests were adapted from Swingle's (1925), Wigglesworth's (1928), Cole's (1928), and Feigl's (1937) techniques. No attempt was made to conduct a differential analysis. Invertase and maltase were present. Neither lipase, lactase, nor amylase were detected. Amylase had been found occurring quite commonly, however (Dirks, 1922; Straus, 1909; Biedermann, 1911 and 1919). Lactase had been reported from some species. Proteases and glycogenase also occur (Uvarov, 1928). It is apparent from the standpoint of the enzymes found present by various workers that phytophagous larvæ are capable of digesting a meat diet. That both proteases and diastases occur in carnivorous insects and phytophagous insects alike is well known.

As seen by the examination of fæces most of the constituents of a meat diet were utilized. Furthermore, all the



dietary requirements for complete development are met by a meat diet. The above considerations coupled with the fact that phytophagous larvæ have been successfully raised to maturity on a meat diet refute the belief that a plant diet is necessary for the well-being of these larvæ.

### III

The following additional reports of cannibalism and the carnivorous habit have been gleaned from the literature.<sup>1</sup> Most of them may be explained on the basis of the principles set forth above and in a previous paper.

Riley, Packard, and Thomas (1883) stated that *Laphygma frugiperda* A. & S. and *Cirphis unipuncta* Haw. resort to cannibalism to satisfy their hunger when migrating. Many individuals are killed in this manner. Aitken and Davidson (1890) reported *Ornithoptera minos* Cram. as eating its own pupæ when normal food was wanting. Witfield (1889) regarded *Papilio ajax* L. as showing more highly developed cannibalistic propensities than any other Papilionid larva of his acquaintance. Floersheim (1909) found, on the contrary, that this species exhibits such behavior only during a shortage of food and then not very readily, since of twenty individuals but two were lost by cannibalism although the food shortage was extreme. Sorhagen (1899) listed all the cases (about eighty) of cannibalism known to him at the time. Forbes (1905) also reported *L. frugiperda* as being cannibalistic in nature when migrating. *Thecla w-album* according to Tutt (1905-1906) is commonly supposed to leave its food in order to feast upon the newly-formed pupæ of its own species. Hering (1926) designated eighty-one species as "Mordraupen" of which nine cases had been reported as occurring in nature. This list is based on that of Sorhagen. Lommatzoch (1926) reported *Spilosoma lubricipeda* Esp. as eating a dead noctuid when its food supply had been exhausted. The report of Junglung (1930) that *Scopelosoma satellitia* L. resorted to coprophagy in captivity when food was lacking is interesting. Small larvæ

<sup>1</sup>Berg's paper quoted in *Psyche* 44(4): 114, 1937 was also reviewed in *Kosmos, Zeit. f. einheitliche Weltanschauung auf Grund der Entwicklungslehre*, 3: 362-363, 1878.

of *Carpocapsa pomonella* L. when crowded exhibit cannibalism (Balduf, 1931). Buckstone (1938) recorded an instance in which the larvæ of *Pieris rapae* L. and ova of *P. brassicae* were confined in the same box. When the latter emerged, they ate the former although the enclosed cabbage leaves were still fresh.

With further regard to cannibalism under natural conditions I am grateful to Dr. H. G. Crawford of the Department of Agriculture, Canada for permission to quote from correspondence with departmental officers in the field.

During the summer of 1938 outbreaks of *Cirphis unipuncta* Haw. occurred but no cannibalism was observed. However, Mr. R. P. Gorham reported that larvæ under laboratory conditions fed on pupæ although they showed no interest in larvæ even when massed together in great numbers. The same officer noticed no cannibalism in *Nephelodes emmedonia* Cram. *Agrotis fennica* Tausch repeatedly attack one another in captivity. Mr. Gorham is of the opinion that most of our common garden cutworms are cannibalistic on pupæ in the laboratory. No cannibalism was observed in *Euxoa ochrogaster* Guen. or *Loxostege sticticalis* L. Mr. K. M. King and Mr. H. L. Seamans report that larger larvæ of *Agrotis orthogonia* Morr. attack smaller and weaker ones especially in the laboratory. *Chizagrotis auxiliaris* Grote according to Mr. Seamans is markedly cannibalistic under conditions of migration. When the advance of the larvæ is checked by some obstacle such as a furrow, the weaker larvæ are quickly attacked. Curiously enough larvæ which have been killed by poisoned bait are frequently eaten.

#### LITERATURE CITED

- Aitken, E. H. and Davidson, J., 1890. Notes on the larvæ and pupæ of some of the butterflies of the Bombay Presidency. J. Bombay Nat. Hist. Soc., 5:362.
- Balduf, W. V., 1931. Carnivorous moths and butterflies. Trans. Illinois State Acad. Sci., 24(2): 156-164.
- 1938. The rise of entomophagy among Lepidoptera. American Nat., 72: 358-379.
- Biedermann, W., 1911. Die Aufnahme, Verarbeitung und Assimilation der Nahrung. Pf. 9. Die Ernährung der Insekten. Winterstein, Handb. vergl. Physiol. 2(1): 726-902.
- 1919. Beiträge zur vergleichenden Physiologie VII and VIII. Pflügers Archiv f. die ges. Physiologie, 174: 358-425.

- Buckstone, A. A. W., 1938. *Pieris rapæ* a cannibal. Entomologist, 71(897): 34.
- Cole, S. W., 1928. Practical Physiological Chemistry. 8th ed., Baltimore.
- Dethier, V. G., 1937. Cannibalism among lepidopterous larvæ. Psyche, 44(4): 110-115.
- Dirks, E., 1922. Liefern die Malpighischen Gefäße Verdauungsekrete? Arch. f. Naturgesch., 4: 161-220.
- Feigl, F., 1937. Qualitative Analysis by Spot Tests, 314-316, N. Y.
- Floersheim, C., 1909. Larval habits of *Iphiclides ajax*. Ent. Rec., 21(5): 113-115.
- Forbes, S. A., 1905. 23d Report State Ent. Illinois, 82.
- Hering, M., 1926. Biologie der Schmetterlinge, 71-75, Berlin.
- Junglung, G., 1930. Ein Fall von Koprophagie (Kotfressen) bei *Scopelosoma satellitia* L. (Lep.). Ent. Zeit. Frankfurt a. M., 43: 57.
- Lommatzoch, W., 1926. Sonderbare Mordegelüste einer Raupe. Int. Ent. Zeit., 20: 232.
- Riley, C. V., Packard, A. S., and Thomas, C., 1883. Third Report of the U. S. Ent. Commission, 117.
- Sorhagen, L., 1899. Mordraupen. Illustr. Zeit. f. Ent., 4(4): 49-51, 4(6): 82-85, 4(9): 135-137.
- Straus, J., 1909. Über das Vorkommen einiger Kohlenhydratfermente bei Lepidopteren und Dipteren in verschiedenen Entwicklungsstadien. Zeit. f. Biol., 52(1-3): 95-106.
- Swingle, H. S., 1925. Digestive enzymes of an insect. Ohio J. Sci., 25(5): 209-218.
- Tutt, J. W., 1905-1906. British Lepidoptera, 8: 37, London.
- Uvarov, B. P., 1928. Insect nutrition and metabolism. A summary of the literature. Trans. London Ent. Soc., 76(2): 255-343.
- Wigglesworth, V. B., 1928. Digestion in the cockroach. III The digestion of proteins and fats. Biochem. J., 22(1): 150-161.
- Witfield, 1889. Scudder's Butterflies of the Eastern United States and Canada, 2: 1273.